

Behavior and sensitivity of an optimal tree diameter growth model under data uncertainty

Don C. Bragg*

USDA Forest Service, Southern Research Station, P.O. Box 3516, UAM, Monticello, AR 71656, USA

Received 7 March 2003; received in revised form 28 April 2004; accepted 30 July 2004

Abstract

Using loblolly pine, shortleaf pine, white oak, and northern red oak as examples, this paper considers the behavior of potential relative increment (PRI) models of optimal tree diameter growth under data uncertainty. Recommendations on initial sample size and the PRI iterative curve fitting process are provided. Combining different state inventories prior to PRI model development increased sample size and diameter class representation while regionalizing the models. Differences arose between loblolly and shortleaf pine in both the contribution from each state inventory pool and the number of points used in the final model fitting. Generally, pooled models predicted the highest overall increment. Natural-origin loblolly pine produced a significantly different PRI model than planted loblolly. PRI curves for northern red oak in the Lake States and the Midsouth varied across the range of diameters considered, suggesting that widespread geographic differences in optimal performance may be present within a species. The PRI methodology is consistent with current theories on diameter growth and compares favorably with other model designs. Published by Elsevier Ltd.

Keywords: Potential relative increment; Ecological model; *Pinus taeda*; *Pinus echinata*; *Quercus alba*; *Quercus rubra*; Eastwide Forest Inventory Data Base (EFIDB)

Software availability

Title: PRI (contains two separate programs, RGR.EXE and MAXARI.EXE)

Developer: Don C. Bragg, USDA Forest Service, Southern Research Station, P.O. Box 3516 UAM, Monticello, AR 71656 USA; tel.: +1-870-367-3464, ext. 18; fax: +1-870-367-1164; e-mail: dbragg@fs.fed.us

First year available: 2001

Hardware requirements: IBM-compatible computer, MS-DOS version 6.6 or Windows 3.1 or higher version; Intel 486 or better CPU; VGA graphics or better

Program language: FORTRAN 90/95

Program size: 313 Kb download (compressed); RGR = 329 Kb, MAXARI = 277 Kb, associated files ~10 Kb (uncompressed) (EFIDB data files can exceed 30 Mb)

Availability and cost: PRI programs are public domain and free for download via the internet at <http://www.srs.fs.fed.us/4106/downloads.htm>.

EFIDB files are available through the USDA Forest Service Forest Inventory and Analysis program

The RGR program calculates actual relative increment of eligible individuals and places these records in an ASCII file. The MAXARI program selects the fastest growing individuals per diameter class and records these in an ASCII file for post-processing in

* Tel.: +1 870 367 3464x18; fax: +1 870 367 1164.
E-mail address: dbragg@fs.fed.us

a statistical package capable of nonlinear regression and iterative deletion of data points. Given the structural dependence of the PRI programs on the EFIDB, species are currently limited to those reported in Hansen et al. (1992). With some formatting modifications, other species are possible (to a total of 999). Up to 1 million tree records from as many as 30,000 plots in 1000 counties can be processed. System performance varies by computer power and input file size. Bragg (2002) processed EFIDB plot and individual tree files containing hundreds of plots and tens of thousands of trees in less than a minute on a 500 MHz Pentium III[®] personal computer with 384 MB of RAM. More detailed information on operating the PRI program suite can be found in Bragg (2002).

1. Introduction

The accurate prediction of tree growth is critical to the modeling of forest dynamics. Many different formulations are available, ranging from quick approximations intended for rapid field application (Herrick, 1938) to much more complicated mathematical approaches (Deetlefs and Du, 1954; see also review in Zeide, 1989). Some growth models rescale optimal diameter increment to determine actual growth (e.g., Botkin et al., 1972; Wu et al., 1994; Bragg, 2001), while others use equations that directly predict increment (e.g., Wykoff et al., 1982; Zeide, 1993; Lynch et al., 1999). Arguments for one design or another can be made, as each has strengths and weaknesses. However, only a few have undertaken the critical evaluation of the design of increment models. Zeide (1993); Shvets and Zeide (1996) decomposed numerous growth models into two general forms (power and exponential decline) and examined their behavior and limitations based on accepted allometric properties of trees. They emphasized that further biomathematical consideration of the growth models could lead to improvements, and thus better forest models. Fleming (1996) questioned the design of specific increment models developed by Duff and Nolan (1957) and suggested that their approximations, while leading to relatively minor errors, could be avoided using improved mathematics. Bragg (2001) challenged the ecological validity of the original gap model optimal increment curves, finding that its design underestimated potential growth because of inappropriately defined functions.

Even these investigations did not thoroughly examine the behavior of increment models given the uncertainty of biological data. Factors like sample size, consistency, and origin of data may influence the outcome so substantially that different outcomes may result. The use of field data means that factors like observer bias, study design and application problems, and subjectivity

in model fitting may also become significant. However, these are not insurmountable problems for increment modeling so long as they are recognized and documented. This paper examines the behavior of the potential relative increment (PRI) optimal tree growth models (Bragg, 2001), focusing on the sensitivity of this method to various levels of data uncertainty and equation manipulation.

2. Methods

2.1. PRI methodology

The PRI approach assumes that individual trees with the greatest periodic growth develop under conditions nearing “optimum.” The principles that guide the PRI methodology were originally expounded by R.A. Webb, who coined the label “boundary line analysis” for the use of extensive data sets to identify the probable upper limit of biological productivity (Webb, 1972). To apply this approach to tree diameter growth, sample size must be large and taken from a spatially extensive database, with adequate coverage of site and stand conditions and diameter distributions. Even with extremely large samples, PRI produces conservative growth models because it is highly unlikely that a tree actually growing under optimal conditions has been included in the inventory. In practical terms, maximum growth projections from PRI compare favorably to those few reported in the silvicultural literature (e.g., Burns and Honkala, 1990a,b). Further information on the PRI methodology, including some possible sources of error and error structures, can be found in Bragg (2001).

2.1.1. Background

The advent of computer models of forest growth that emphasized mechanism (e.g., Botkin et al., 1972) altered the nature of forest-based ecological prediction. One novel feature of many of these simulators was a new increment strategy based on individual tree growth performance scaled by limiting conditions. This design soon dominated forest dynamics models (Dale et al., 1985), even those developed separately from the popular gap models (e.g., Chertov, 1990; Martin and Ek, 1984; Phipps, 1979). Conceptually, growth rescaling represented an advance because it allowed for the manipulation of state conditions to improve our understanding of physiological and/or ecological responses to a varying environment. Note that even though the recent advent of rapid computer analysis and simulation modeling has made optimal diameter growth prediction commonplace, this is not a new concept: Graves (1906, p. 273) outlined the value of and a procedure to determine maximum growth from inventory information.

The literature on the environmentally constrained strategy has labeled the core growth model “potential” or “optimal.” For instance, Reed (1980) and Dale et al. (1985) applied the terms optimal and potential to refer to maximum increment equations. Given that the semantic definitions of optimal (“most desirable or satisfactory”) and potential (“capable of development to actuality”) (Mish, 1984) have been blurred by their technical use in natural resources, I will use them interchangeably. Hence, optimal increment models yield potential growth when the environmental factors influencing them are maximally favorable.

The PRI methodology estimates optimal growth as a function of species and current tree diameter. The PRI model is a derivative of Hoerl’s special function (HSF) (Hoerl, 1954, p. 64):

$$Y = aX^b e^{cX} \quad (1)$$

where the base of the natural log component (e^c) has been replaced with a single parameter d to yield the final PRI form:

$$Y = aX^b d^X \quad (2)$$

Both forms of HSF are generalizations of the power (when $c=0$ or $d=1$) and exponential (when $b=0$) functions (Sit and Poulin-Costello, 1994). Sit and Poulin-Costello (1994, p. 60) advocated the use of the first form (Eq. (1)) of HSF because “... [the] model is more specific and has better statistical properties than that of Type I [Eq. (2)] ...”. Their primary concerns with Eq. (2) were that d^X was undefined for many values of $d < 0$ and that it was less flexible than Eq. (1) (Sit and Poulin-Costello, 1994, p. 58). However, for the purposes of determining optimal tree diameter growth models, neither objection was of critical importance if Eq. (2) is properly constrained. Eq. (2) is also easier to interpret for this work because of its relative simplicity.

Certain limitations on the regression parameters are necessary for the biologically appropriate application of Eq. (2) with the PRI methodology. First, parameters a and b must be positive values >0 to ensure that negative or zero growth would not occur (intuitively, plants have positive growth, especially under optimal conditions). Additionally, $0 < d < 1$. The d parameter constrains growth as a function of diameter, so if $d > 1$, very large trees would eventually grow at an increasing rate. Such a response would run counter to current interpretations of diameter growth (Zeide, 1993; Shvets and Zeide, 1996) that hold relative increment for big trees as a declining function. HSF is also consistent with Zeide’s requirements for effective diameter growth models (Zeide, 1993; Shvets and Zeide, 1996). Zeide proposed that growth models should include both expansion and contraction components to represent the elevated increment of young trees and the restrained

growth of older individuals. The PRI implementation of HSF retains these features, with expansion (X^b) and contraction (d^X) terms.

Setting the first derivative of Eq. (2) equal to zero and solving for X yields the maximum diameter increment:

$$X = -\frac{b}{\ln(d)} \quad (3)$$

Typically, the diameter of maximum increment is early in the life of a tree, when the increase in plant biomass from one period to the next dramatically increases relative to its initial size.

Although reported in several key texts (e.g., Daniel and Wood, 1980; Wenger, 1984), Hoerl’s special function has not been extensively used in natural resource modeling. Avery and Burkhart (1983) presented the general form in their text on forest measurements. HSF has been incorporated in a bole taper equation (Kozak, 1988), a tree height growth modifier (Donnelly et al., 2001), and possibly a stand volume predictor (Huang et al., 2003). To the author’s knowledge, HSF has not been used to predict individual tree optimal diameter growth even though HSF has favorable statistical and ecological properties for this application. For instance, Sit and Poulin-Costello (1994) noted that the estimated parameters are close to unbiased and normal, with minimum variance. Additionally, the function’s general but complicated form allows for many different curve shapes to be generated with the same equation (Fig. 1). This aspect is advantageous when predicting the behavior of a large number of often differently responding taxa.

2.1.2. Data source and development

Data for this paper were taken from the Eastwide Forest Inventory Data Base (EFIDB) of the USDA Forest Service (Hansen et al., 1992). The EFIDB contains inventory records for all of the states in the eastern US. Comma-delimited ASCII files containing both plot (EFIDB record type 20) and individual tree (EFIDB record type 30) data were analyzed using software written by the author (Bragg, 2002). These programs merge the plot and tree data, calculate actual relative increment (see below), and select the highest actual relative increment values for final derivation of the PRI models.

Loblolly (*Pinus taeda* L.) and shortleaf pine (*P. echinata* Mill.) were selected for most of this paper because of their commercial importance in the southern United States (Baker and Langdon, 1990; Lawson, 1990). Their abundance also makes them good candidates for the PRI methodology. Loblolly pine information was taken from the Arkansas, Louisiana, and Texas EFIDB inventories, while shortleaf pine data were from

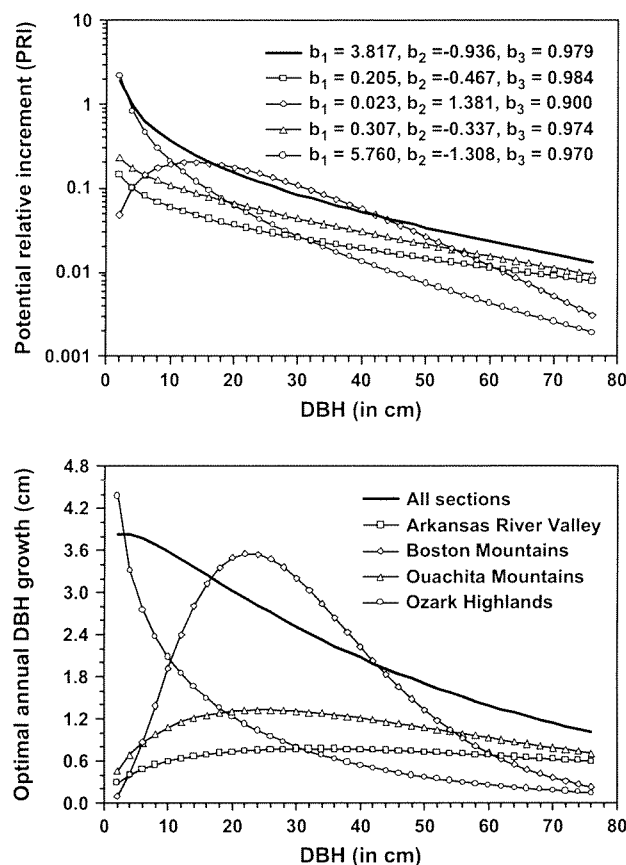


Fig. 1. An example of curve shape possibilities using Hoerl's special function constrained for PRI models. Curves were adapted from Bragg and Guldin (2003) for white oak in different ecoregions of the Interior Highlands of Arkansas, Missouri, and Oklahoma.

Arkansas, Louisiana, and Missouri. For a regional comparison of PRI results (i.e., northern Lake States (Michigan, Minnesota, and Wisconsin) versus the Mid-south (Arkansas, Louisiana, Missouri, and Oklahoma)), northern red oak (*Quercus rubra* L.) was chosen because it is common to both areas.

2.1.3. Relative increment calculation

The first step in deriving PRI models is the calculation of actual relative increment (ARI). ARI is a derivation of a simple interest formula (Avery and Burkhart, 1983):

$$ARI = \frac{DBH - DBH_0}{DBH_0} (P/t) \quad (4)$$

which uses current diameter at breast height (DBH), DBH at the last inventory (DBH_0), P is the period (in years) over which the growth is to be forecast ($P=1$ for an annual design), and t is the remeasurement interval (in years) of the inventory. ARI represents the periodic rate of DBH change given the species and initial size of the tree (Fig. 2a). After calculating ARI, a different program selects the highest ARI scores per 2 cm DBH

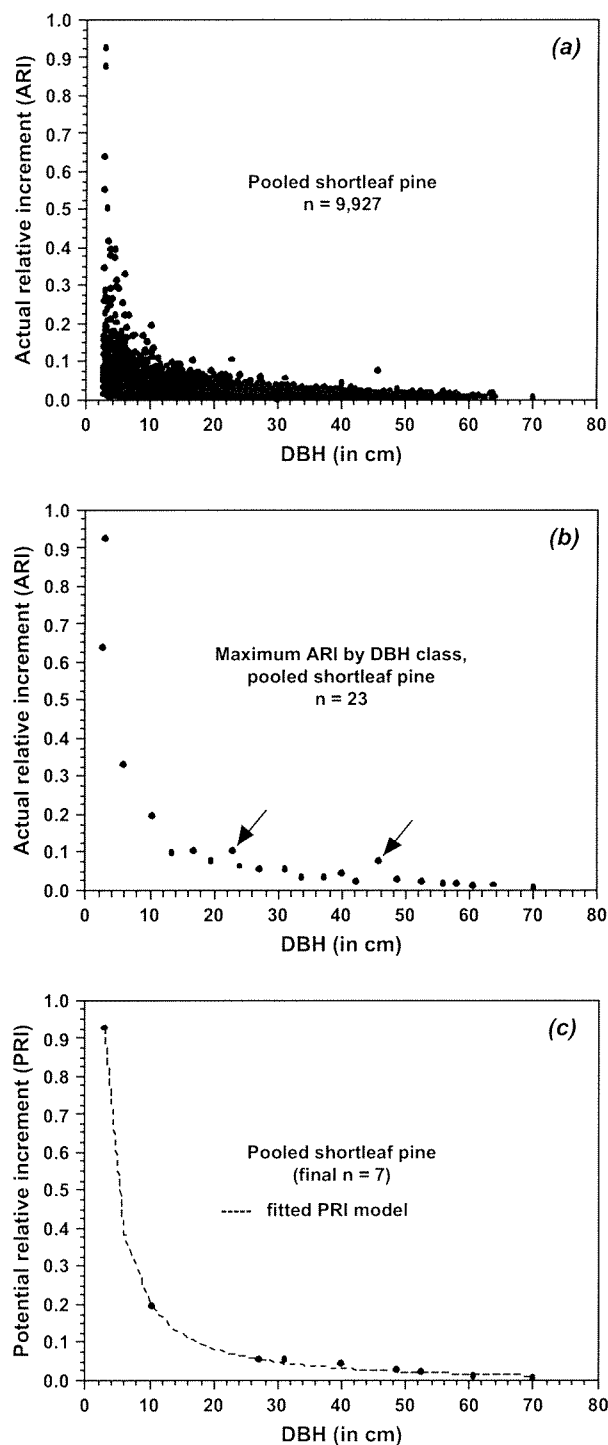


Fig. 2. Steps in the derivation of the PRI optimal diameter models. Actual relative increment is first calculated for the entire sample (a). A subset of these points is chosen to represent the maximal ARI for that DBH class (b). At this stage, outliers (indicated by arrows) are readily identifiable. Only the highest of the maximal points are retained for the final model fitting (c), producing a characteristic PRI curve.

size class (Fig. 2b). The preliminary number of maximal ARI scores retained for model fitting depended on species and the distribution of the sample, but often ranges from 10 to 50 individuals.

PRI model fitting is an iterative process using nonlinear ordinary least squares regression. The final subset was entered into a statistical analysis package and fit to:

$$\text{PRI} = b_1 D_{\text{MAX}}^{b_2} b_3^{D_{\text{MAX}}} \quad (5)$$

where D_{MAX} is the DBH of a tree growing at maximum increment within a predetermined size class and b_1 to b_3 are species-specific parameters. Once the regression parameters have been determined, optimal diameter increment (I_O) can be predicted by substituting current DBH for D_{MAX} and then multiplying this DBH by Eq. (5):

$$I_O = \text{PRI} \times \text{DBH} \quad (6)$$

Realized increment (I_R) is then determined by rescaling I_O with environmental quality modifiers. For instance, the classical gap model approach multiplicatively applies a set of modifiers (M):

$$I_R = I_O \left(\prod_{i=1}^n M_i \right) \quad (7)$$

Any response function(s) can be used to produce M_i , which traditionally ranges from 0 (prohibitively poor environment) to 1 (optimal). The practice of fertilization or irrigation could be addressed entirely within the multipliers, even if some would exceed the upper threshold (i.e., $M_i > 1$), without impacting the application of PRI. This, of course, presumes that the modifying functions are capable of such a fundamental shift in site quality, especially if the treatment's impact is transitory or compensatory.

The PRI curve fitting process is rules-based, with the objective of identifying a subset of points that best reflects individual performing at their apparent maximum given their initial size. Most of the points removed from the analysis did not fall along the optimal curve (Fig. 2c). Others were deleted because they appeared so far out of line with the rest of the data as to suggest an outlier (Bragg, 2001). Outlier detection is a key feature of the PRI methodology. For example, Bragg (2004) reported an 80 cm DBH black cherry (*Prunus serotina* Ehrh.) and an 80 cm DBH white oak (*Quercus alba* L.) that were reported to have grown approximately 27 cm in DBH over 12 years. This growth rate, though possible for a young and vigorous individual of either species, is highly dubious in trees of this size. These individuals were quickly identified by the PRI process as questionable, and given their possible influence on the increment models, were removed from the data before the final curves were fitted.

It also is occasionally necessary to introduce a new “beginning point” (i.e., the smallest DBH point defining

the curve) if the tree in the smallest diameter class fails to match the trend suggested by the other maximum ARI points. The extremes of the diameter range are almost always the most problematic aspect of forest inventories based on point-sample estimates of commercial forest species in modern landscapes, as small trees are routinely undersampled and few very large specimens remain.

2.1.4. Comparison of PRI with other diameter increment approaches

Zeide (1993) reviewed 12 models of diameter growth, all of which were some version of a power or exponential function. His objective was to fit growth models to inventory data, so his conclusion that “... the growth path is inherently imprecise and can be viewed as a wide valley rather than a single line ...” (Zeide, 1993, p. 594) is essentially correct. This fitting of a curve directly to inventory data without consideration of the factors associated with growth performance is one possible means to predict increment. A more complicated but related design that interprets deviations from a mean growth level as a function of stand and site quality can be found in some empirical models (e.g., Wykoff et al., 1982; Lynch et al., 1999). The Forest Vegetation Simulator (FVS) (Wykoff et al., 1982) presents a good example of this approach. FVS predicts periodic realized increment with the following model:

$$I_R = \sqrt{\text{DIB}^2 + \text{DDS}} - \text{DIB} \quad (8)$$

where DIB is inside bark DBH and the change in double inside squared diameter (DDS) equals

$$\begin{aligned} \text{DDS} = \exp \bigg(& \text{HAB} + \text{LOC} + b_1 \cos(\text{ASP}) \text{SL} + b_3 \text{SL} \\ & + b_4 \text{SL}^2 + b_5 \text{EL} + b_6 \text{EL}^2 + b_7 \frac{\text{CCF}}{100} + b_8 \ln(\text{DBH}) \\ & + b_9 \text{CR} + b_{10} \text{CR}^2 + b_{11} \frac{\text{BAL}}{100} + b_{12} \text{DBH}^2 \bigg) \quad (9) \end{aligned}$$

In Eq. (9), HAB is an intercept dependent on habitat type; LOC is an intercept based on location, ASP is stand aspect (in degrees), SL is stand slope ratio, EL is stand elevation (in feet), CCF is stand crown competition factor, CR is crown length ratio, BAL is basal area (ft^2/ac) of trees larger than the subject tree, and b_1 to b_{12} are species-specific regression coefficients. Both the Zeide and FVS approaches to growth modeling directly predict actual increment, so any factor(s) influencing realized performance have already been imbedded into the models. The rescaled optimal approach differs in that actual growth is a function of a predicted optimal increment and modifier(s) that limit growth. The

JABOWA model (Botkin et al., 1972) typifies this approach:

$$I_R = \frac{G \times \text{DBH} (1 - (\text{DBH} \times \text{HT} / \text{DBH}_{\text{MAX}} \text{HT}_{\text{MAX}}))}{274 + 3b_2 \text{DBH} - 4b_3 \text{DBH}^2} \prod_{i=1}^n M_i \quad (10)$$

where G is a species-specific growth parameter, HT is current tree height, DBH_{MAX} and HT_{MAX} are species-specific DBH and height maximums, respectively, b_2 and b_3 are fitted regression parameters, and there are n environmental modifier functions (M_i) acting upon this model. The ability to customize growth response makes the optimal rescaling approach popular in ecological modeling.

Not all approaches to optimal tree growth consider diameter increment. Phipps (1979) modeled tree performance as a function of ring width growth, which can be used to directly infer diameter increment. Pan and Raynal (1995) evaluated volumetric increment as the measure of performance based on environmental factors and previous productivity, while Chertov (1990) predicted biomass increment. While these studies use different measures of productivity, they are still based on the principle of rescaling growth downward from presumably optimal growing conditions to arrive at realized increment.

2.1.5. The biological behavior of PRI

Numerous studies have found that increment depends on tree size and responds non linearly over time (Deetlefs and Du, 1954; Assman, 1970; Wykoff et al., 1982; Vanclay, 1988; 1994; Zeide, 1993; Maclean and Scott, 1988; Black and Abrams, 2003). Maclean and Scott (1988) concluded that simple linear interpolation was inadequate to explain increment from one inventory to the next for many species. Given what is known about tree growth, sustained linear incremental change is counter-intuitive. Simple geometry forces the diameter increment to decline at a nonlinear rate because new layers of sapwood must be partitioned around an increasingly larger core. The power function-based design of PRI and other designs (e.g., Shvets and Zeide, 1996) fits this attribute of tree growth performance well by maximizing increment early in the life of a tree and then tapering off response with increasing size (or age).

2.2. PRI model fitting suggestions

Since ordinary least squares regression (OLS) was used to derive the PRI models, the assumptions associated with OLS also apply to the models. Some additional guidance can make the process of fitting PRI models more efficient and reliable. These “rules-of-

thumb” are not absolute, inviolable edicts but rather general suggestions.

First, as with any empirically based model fitting exercise, the more data, the better the outcome. Although greater than 1000 individuals per species are preferred for PRI analysis, a minimum of 100 is recommended. As an example, Bragg (2001) tallied 134,881 individuals for 24 species. Some species had more than 10,000 trees, with only eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch) and pin cherry (*Prunus pennsylvanica* L.) totaling less than 1000 (998 and 107, respectively). Even though a single state’s inventory usually assures adequate sample sizes, merging two or more inventory areas (if sufficiently similar) to boost sample sizes may be necessary (Bragg, 2001; 2003).

Individuals should also be drawn from across as much of the expected DBH distribution as possible, with all size classes being represented by multiple records. This is critical because of the limited subset used to fit the final models, but may prove difficult due to the scarcity of big trees in most forest inventories (Bragg, 2001; 2003). A minimum of five well-distributed points when fitting parameters is recommended, especially across the middle range of the diameter distributions. Note that retaining too many points may underestimate optimal growth (see Section 3.3).

Due to the way the PRI methodology is applied, small errors in the upper DBH range can noticeably influence the shape of the entire PRI curve (Bragg, 2001). Since the fitting process permits the adjustment of the curve based on which points remain in the regression, it is possible to retain a set to closely fit the largest diameter trees and thus constrain errors in other portions of the size class range. However, with very small sample sizes, PRI may fit curves that over-emphasize growth of large trees and discount the performance of small trees.

Table 1
Summary of loblolly and shortleaf pine initial data used to derive PRI models

Species	State	<i>n</i>	Minimum DBH (cm)	Mean DBH (cm)	Maximum DBH (cm)	Standard deviation (cm)
Loblolly pine	Arkansas	11340	2.8	22.4	88.6	13.5
	Louisiana	12807	2.8	26.7	103.4	14.1
	Texas	11950	2.8	26.1	102.4	15.4
	Total	36097				
Shortleaf pine	Arkansas	7,587	2.8	26.0	70.1	10.6
	Louisiana	1393	2.8	26.4	63.8	10.3
	Missouri	947	2.8	21.0	51.6	10.1
	Total	9927				

3. Results and discussion

3.1. Influence of pooling on model fitting

Several interesting trends can be found by comparing the models derived from different inventories. Table 1 summarizes the diameter distributions by species and state. When aggregated, both loblolly and shortleaf pine produced large samples (36,097 and 9927 trees, respectively). Ideally, pooled samples for a regional model would be consistent with the evenness of the loblolly pine distribution: Arkansas contributed 31.4% of the total, Louisiana provided 35.5%, and Texas yielded 33.1%. However, this level of equity does not always happen. Shortleaf pine produced a considerably more skewed pattern: 76.4% of the trees were from Arkansas, 14.0% came from Louisiana, and only 9.5% of the final total was from Missouri. Even though this biases the shortleaf pine PRI model towards the sample from Arkansas, it does not necessarily invalidate the use of pooling, especially when very few individuals of a given species are available.

Bragg and Guldin (2003) segregated white oak EFIDB records from the Interior Highlands of Arkansas, Missouri, and Oklahoma into four ecoregions (Ouachita Mountains, Arkansas River Valley, Boston Mountains, and Ozark Highlands) and found substantial differences in PRI models derived for each region and a pooled model of the entire Interior Highlands data set (Fig. 1b). They speculated that while notable differences could have arisen from ecophysiological causes, the most likely explanation lay with the inconsistent distribution of the data by ecoregion and diameter class. One of the biggest problems in any method of fitting optimal growth curves to inventory data is the absence of some size classes (Bragg, 2001). Most individuals in the EFIDB are small- to moderate-sized trees, with few in the largest classes (see Fig. 3; Bragg, 2001). Aggregating geographically, ecologically, and genetically similar populations from multi-state or multi-region inventories allows for the extension and supplementation of DBH classes. In the present study (Table 1), pooling increased the sample range (maximum DBH rose from 88.6 to 103.4 cm for loblolly pine, and from 51.6 to 70.1 cm for shortleaf pine) while supplementing many poorly represented size classes with additional observations.

Aggregating inventories may also be required to fully portray the potential growth of a species. Bragg (2001) found that pin cherry data from the Lake States were insufficiently represented to derive a reasonable optimal growth model. Further records from New York, Pennsylvania, and West Virginia were used to supplement the original pool, and thus better results were achieved (Bragg, 2001). In a separate effort, optimal growth models were developed for the Midsouth (Bragg,

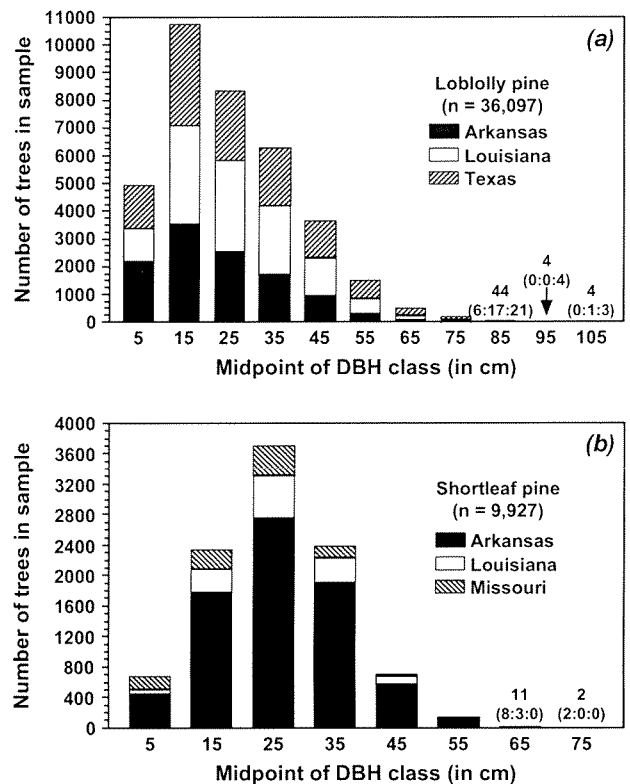


Fig. 3. Apportionment of loblolly (a) and shortleaf (b) pine pooled samples by state inventory. For the largest diameters, the scale was inadequate to show the ratios found, but the number above the DBH class midpoint represents the Arkansas, Louisiana, and Texas and Arkansas, Louisiana, and Missouri tallies for loblolly and shortleaf pine, respectively.

2003). A number of species originally considered were eventually discarded because very few individuals were found (often <10 trees), even after the inventories from five states (Arkansas, Louisiana, Missouri, Oklahoma, and Texas) were combined. In cases where uncommon species are to be modeled, the inclusion of increment information from other sources is strongly encouraged if the EFIDB has too few records. Other supplemental sources and field sampling could be used to boost sample size and extent, even for relatively common taxa.

3.2. PRI models by species

Optimal PRI models followed unique trajectories based on the inventory from which they were derived (Table 2, Fig. 4). All designs decreased continually over the diameter range considered (Fig. 4a). However, the differences in the curves resulted in variable increment results (Fig. 4b). For instance, maximal diameter growth varied as a function of tree size. The Arkansas optimal growth curve (Fig. 4b) declined monotonically throughout the diameter range, while all other fitted curves produced skewed modal shapes that peaked at 15–20 cm DBH. At the smallest DBH (2 cm), the PRI curve from

Table 2

Fitted nonlinear PRI parameters and their corresponding standard errors (SE) by species and state

Species	State	b_1 (SE)	b_2 (SE)	b_3 (SE)	n^a
Loblolly pine	Arkansas	2.671599 (0.04700)	−0.99814 (0.0149)	0.9909 (0.0010)	23
	Louisiana	1.330230 (0.05346)	−0.67017 (0.0333)	0.9782 (0.0016)	19
	Texas	1.261242 (0.13820)	−0.35368 (0.0942)	0.9587 (0.0065)	10
	Pooled (one) ^b	1.958836 (0.06879)	−0.64679 (0.0319)	0.9755 (0.0021)	8
	Pooled (top 3) ^b	1.592023 (0.03915)	−0.59771 (0.0215)	0.9721 (0.0011)	13
Shortleaf pine	Arkansas	1.171748 (0.12656)	−0.62399 (0.09728)	0.9622 (0.0040)	25
	Louisiana	0.395645 (0.04257)	−0.33194 (0.08697)	0.9692 (0.0067)	8
	Missouri	2.971630 (0.18203)	−0.89714 (0.08200)	0.9413 (0.0096)	8
	Pooled	3.537060 (0.28381)	−1.20650 (0.07810)	0.9947 (0.0027)	9

All parameters were significant at a $p < 0.05$. Pooled parameters resulted from the aggregation of the state inventories by species, followed by nonlinear model fitting.

^a The final number of points used to generate parameters.

^b Pooled (one) represents the customary one maximum ARI point per size class model fitting, while the values for the Pooled (top 3) row were derived from averaging the ARI scores of the 3 highest points per size class.

Arkansas produced the greatest potential annual increment. However, the model for Texas rapidly overtook the others (except the pooled curve) from about 5 cm DBH until ~55 cm DBH, after which its steep rate of descent dropped it below the Arkansas curve, and at 64 cm DBH it fell below the Louisiana

curve. The Louisiana model produced the lowest overall increment from 2 to 12 cm DBH and from 42 to 64 cm DBH. Interestingly, the pooled curve did not always yield the highest potential increment (Fig. 4b). In fact, except for the 4–8 cm DBH range and from 34 to 72 cm

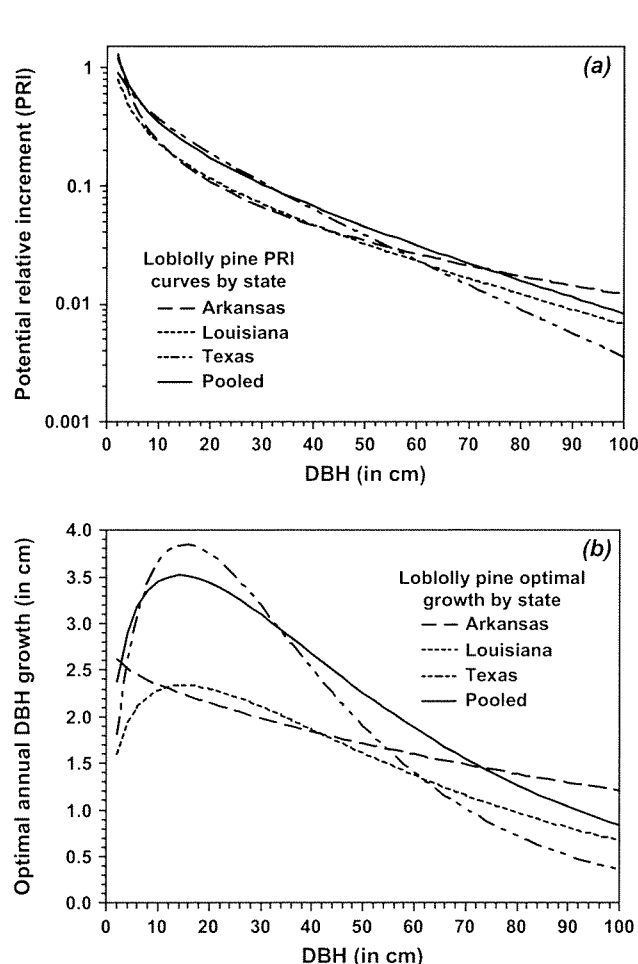


Fig. 4. Loblolly pine PRI curve (a) and optimal annual increment (b) curves by state inventory and pooled results.

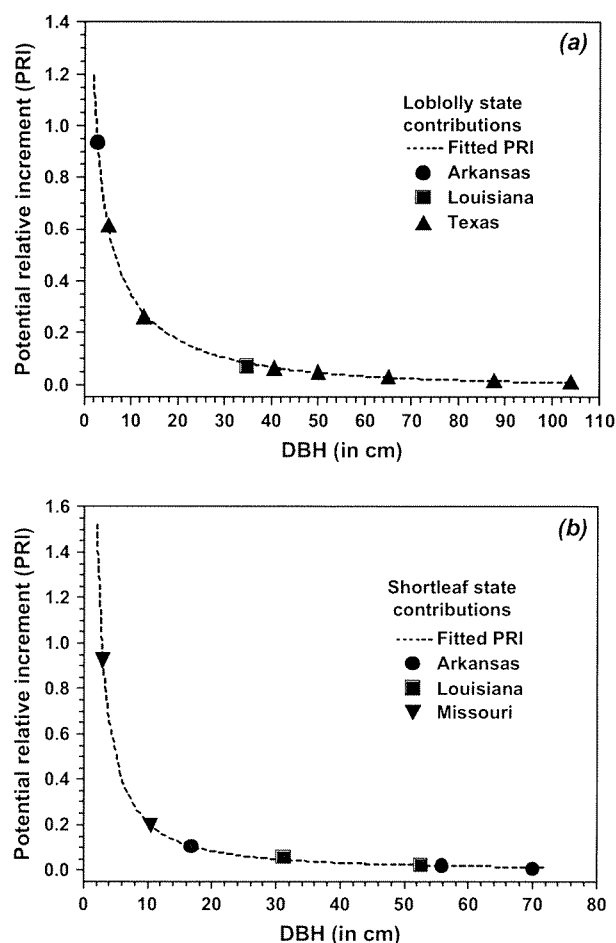


Fig. 5. Pooled PRI curves, showing individual points from different state inventories used to fit the models for loblolly (a) and shortleaf (b) pine.

DBH, either the Texas or Arkansas models predicted greater growth.

The loblolly pine pooled PRI model, when separated by inventory into the final number of points selected, included a preponderance of Texas records (Fig. 5a), with only one point coming from both Arkansas and Louisiana. The true significance of this Texan bias is uncertain, however, because many of the deleted points from the other states differed little from the Texas records. While it is possible that localized climatic, topoedaphic, or genotypic differences could result in consistently higher growth in Texas, the limited number of final points samples makes it virtually impossible to determine if this artifact arose from sampling, chance, or regionally biased factors.

Shortleaf pine provides a different example of PRI model behavior. A relatively even distribution (Fig. 5b) of the final sampling points (3 from Arkansas, 2 from Louisiana, and 2 from Missouri) for shortleaf pine suggests more regional equity in model derivation than for loblolly. Nevertheless, PRI plots indicated considerable differences between the inventories, especially for

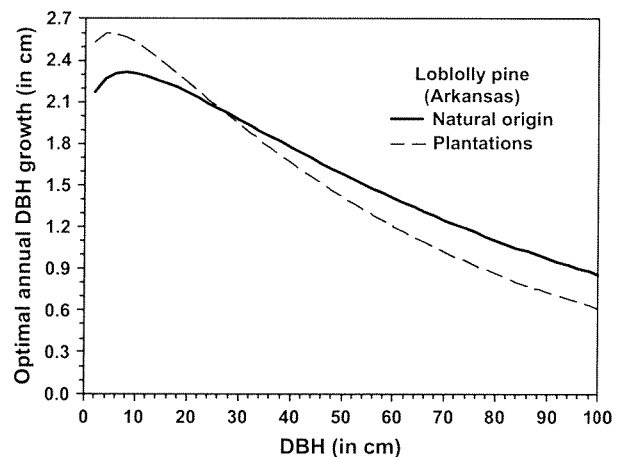


Fig. 7. Comparison of the PRI curves for natural versus planted loblolly pine in Arkansas.

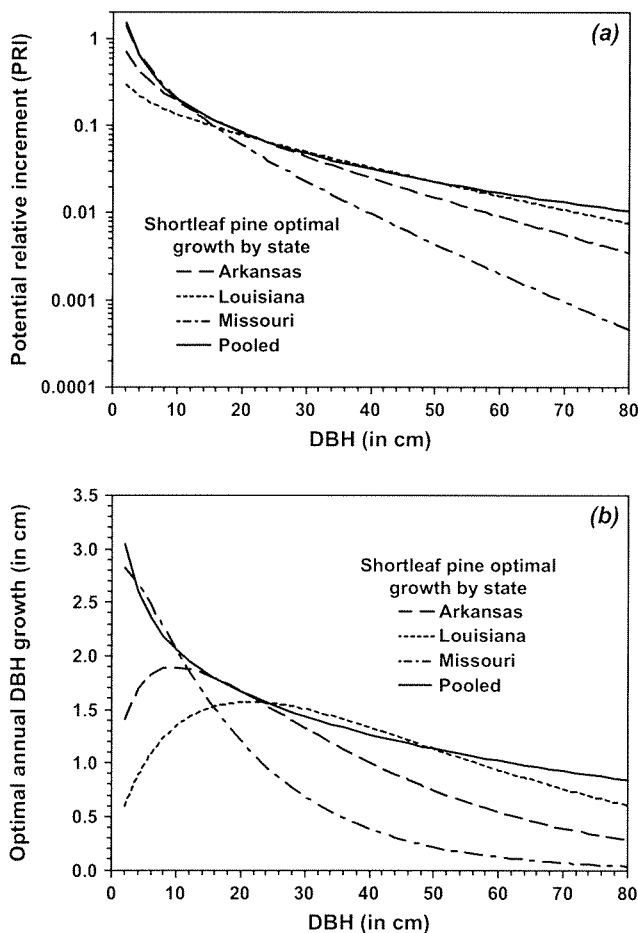


Fig. 6. Shortleaf pine PRI (a) and optimal annual increment (b) curves by inventory.

the Missouri and Arkansas models (Fig. 6a). Translated to optimal diameter increment, the Missouri and pooled models both produced monotonically declining curves, while the Arkansas and Louisiana designs were modal (Fig. 6b). Arkansas shortleaf pine optimal increment was predicted to peak when the trees are about 10 cm DBH, while shortleaf pine in Louisiana maximized at much larger sizes (~ 25 cm DBH). Missouri shortleaf peaked immediately (at the smallest DBH) and dropped off precipitously, so that by ~ 16 cm DBH, it was outperformed by the Arkansas and Louisiana models. The Arkansas PRI model produced the greatest increment from about 12 to 25 cm DBH, after which the Louisiana model predominated. The pooled model behaved more consistently for shortleaf than loblolly pine by producing higher increment than the other shortleaf PRI models, with only occasional instances where individual state models predicted greater increment.

3.3. Variation in PRI model performance

3.3.1. Natural versus planted loblolly pine optimal growth

Differences in PRI model performance may also be sensitive to stand origin. In theory, improved planting stocks are bred to express a greater increment over at least the initial portion of their diameter growth. Fig. 7 compares loblolly pine optimal increment predictions after segregating by stand origin (planted versus natural). For smaller (< 25 cm) trees, the plantation loblolly outperformed natural-origin stands by as much as 0.3 cm annually. This trend reversed for larger loblolly, with natural-origin pines displaying the greatest increment potential.

Though visually disparate, are the natural versus planted PRI models truly different? The nonlinear extra

sum of squares method can be used to find statistically significant differences between nonlinear regression models (Bates and Watts, 1988). As an example, Huang et al. (2000) used nonlinear extra sum of squares to determine if multiple regional height–diameter models for white spruce (*Picea glauca* (Moench) Voss) were necessary, or if a single global model was more appropriate. This approach inserts an indicator variable (χ) into the “reduced” (Eq. (5)) form of the equation, producing a “full” version (PRI_F):

$$PRI_F = (b_1 + a_1\chi) D_{MAX}^{(b_2 + a_2\chi)} [(b_3 + a_3\chi)^{D_{MAX}}] \quad (11)$$

where a_1 , a_2 , and a_3 are parameter estimates for the indicator variable that delimits natural ($\chi=1$) and planted ($\chi=0$) loblolly pines. From these versions of the equation, a ratio of error sum of squares (SSE_R = reduced, SSE_F = full) to degrees of freedom (df_R = reduced, df_F = full) is used to produce an F -test statistic:

$$F = \frac{SSE_R - SSE_F}{df_R - df_F} \div \frac{SSE_F}{df_F} \quad (12)$$

which, if greater than $F_{critical}(\alpha=0.05; df_R - df_F, df_F)$, results in the rejection of the null hypothesis of no difference between the models.

Table 3 lists the error sum of squares and degrees of freedom for the full and reduced models. Eq. (8) produced an F -value = 25.22, which is considerably higher than the $F_{critical}(\alpha=0.05, 3, 34) \approx 2.88$. Hence, the curves shown in Fig. 7 are significantly different, suggesting that the PRI models derived from these Arkansas loblolly pine stands of natural and planted origin are statistically unique.

The nonlinear extra sum of squares test could be applied to most other PRI comparisons (e.g., pooling of state inventories, or final number of trees to fit curves with), however, the appropriateness of this test must remain in context. Unlike most applications (e.g., Huang et al., 2000), PRI models are fit to a very limited number of data points, and given their close fit, significant differences between even very similar curves are almost assured. Additionally, even though the significant differences in Fig. 7 may reflect a trade-off between small and large diameter growth behavior, a sparse sample of planted loblolly pine larger than 60 cm DBH could also have produced the observed trend. Furthermore, inconsistent silvicultural practices and the evolution of planting stock may also lead to a bias in

potential increment outcome, especially if younger (and, presumably, smaller diameter) loblolly pines reflect well-thinned, high-generation improved stock and older plantations are of early generation (or natural) stock that may not have been intensively thinned. Unfortunately, detailed stand history (including seedling origin) and management behavior are rarely available in publicly documented inventories.

3.3.2. Number of points selected

Further understanding of PRI derivation is apparent in the shape of the curves produced when using different numbers of maximal ARI values. With the original number (20) of loblolly pine maximal ARI points from the Texas inventory, potential increment (3.4 cm at 12–14 cm DBH) declines to about 0.2 cm in 100 cm DBH trees. Reducing the number of maximal ARI points affected the shape of the PRI curve (Fig. 8a), which translates into different increment predictions (Fig. 8b). With 10 points, maximum increment (~ 3.8 cm) occurs in slightly larger trees (15–17 cm DBH) and remains noticeably higher for most of the diameter

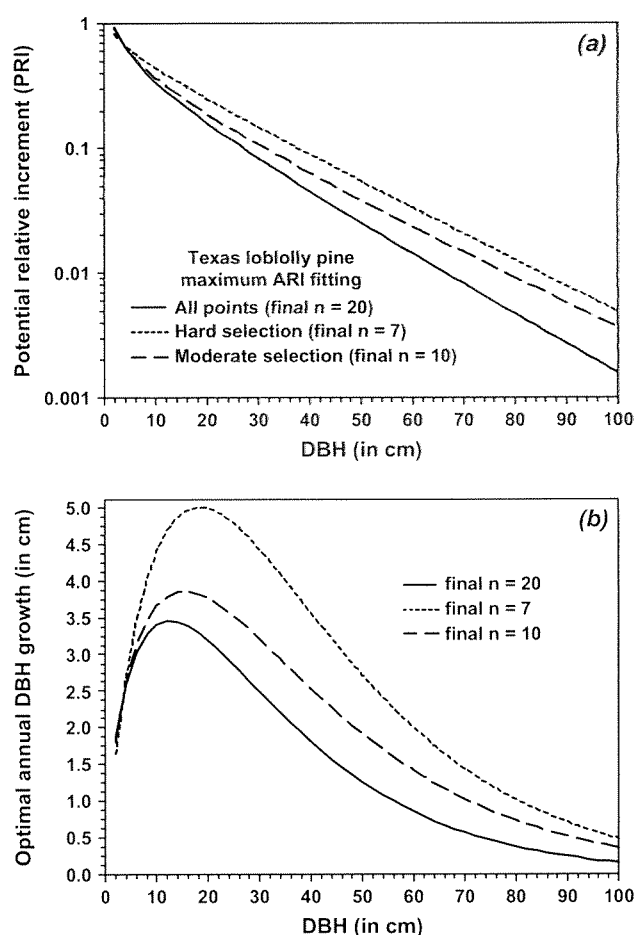


Fig. 8. Fitted PRI curves (a) and optimal annual DBH increment (b) for different final loblolly pine data point set sizes taken from the Texas EFIDB inventory.

Table 3

Statistics used to calculate F -test between natural and planted Arkansas loblolly pine PRI curves

Full model		Reduced model		n	F -value (calculated)
df_F	SSE_F	df_R	SSE_R		
34	0.01500	37	0.00465	40	25.22

range, with 100 cm DBH individuals having a potential annual increment of 0.4 cm. Removing just 3 more points produces an even more pronounced change in curve shape. Under this scenario, annual optimal growth increased to almost 5 cm at 18–20 cm DBH, and trees of 100 cm DBH have a maximum growth of 0.5 cm. The greatest difference in predicted increment between the strongly reduced version and the original and moderately reduced models approached 1.6 and 1.2 cm, respectively. These disparities decreased with increasing tree diameter so that the optimal annual increment did not vary by more than 0.3 cm when the tree reached 100 cm DBH. However, the difference still translates into 25–150% higher growth from the most reduced model.

A possible alternative to the customary approach for deriving PRI models would be to run the regression on multiple data points per size class. This subset could either be a statistically determined fraction of the points (e.g., quantile regression) or a fixed number of points. The primary advantages to using a top-averaging approach include less arbitrariness in suboptimal and outlier point deletion and the incorporation of more data in the model (thus, less sensitivity to the number of points used in fitting). However, top-averaging inevitably reduces the magnitude of optimality by fitting the curve lower than the absolute maximal increment. To illustrate the differences in these approaches, a nonlinear regression model using the average of the top three ARI scores by size class for loblolly pine in the Midsouth was developed (for size classes with <3 points, every datum was used to average).

Fig. 9a plots the top-averaged and pooled models fit to loblolly pine (Table 2). The top-averaged design yielded consistently lower growth performance throughout the diameter distribution. Translated to optimal diameter increment (Fig. 9b), the curves, while similarly shaped, differed notably in their magnitude, with the top-averaged curve ranging from 0.2 cm to 0.4 cm lower than the single maximum point model. Peak increment still occurred at the same DBH (14 cm), with the top-averaged design predicting an optimal increment of 3.1 cm and the single maximum point model forecasting a peak increment of 3.5 cm.

Besides a minimum number of individuals to express the shape of a complex curve, there is no absolute rule about the appropriate number of fast-growing trees for derivation of PRI models. In general, the more data used, the more conservative the estimate of potential increment. After all, if the entire sample is included, the outcome is simply a regression about the mean. For some purposes, a more conservative PRI model (i.e., one that predicts lower optimal growth) is preferable. This is especially true if the data were prone to measurement or transcription error, or there was insufficient quality control to feel confident in the inventory. A more

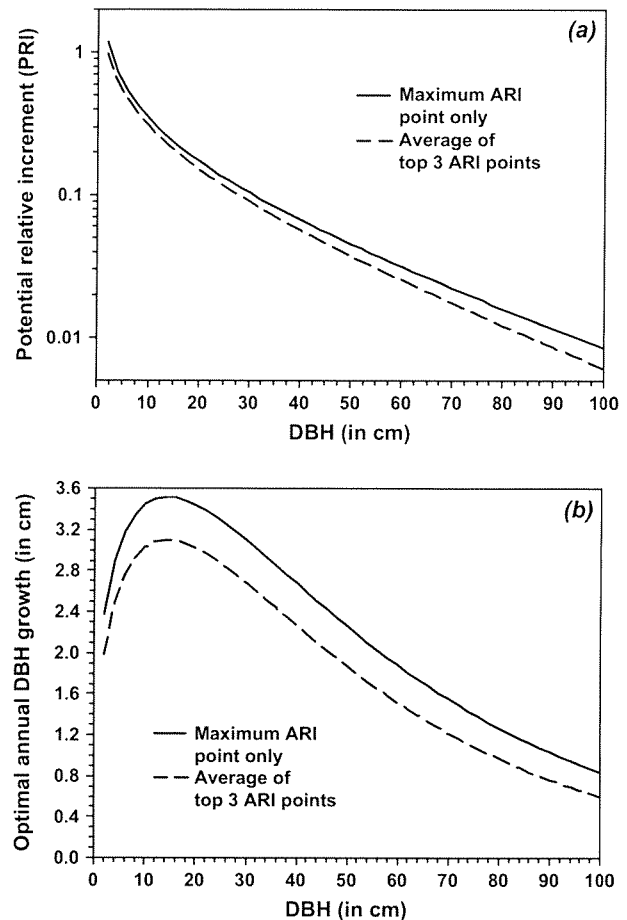


Fig. 9. Contrasts between PRI curves (a) fit for top-averaged (dashed line) and the customary single maximum point design (solid line) for the same Midsouth loblolly pine data. Even though the optimal increment curve shapes differed little, the magnitude of the response was 0.2–0.4 cm less for the top-averaged curve.

aggressive PRI model uses fewer trees to define the curve, providing a better approximation of the biological potential of a species. Yet, a low number of maximal points also increases the likelihood that an incorrectly measured data point will influence curve shape.

Table 4

Northern red oak PRI parameter (and standard errors (SE)) from northern (Michigan, Minnesota, and Wisconsin) and southern (Arkansas, Louisiana, Missouri, and Oklahoma) EFIDB inventories

Sample area (total <i>n</i>)	b_1 (SE)	b_2 (SE)	b_3 (SE)	Final <i>n</i>
Northern (6906)	2.241167 (n/a) ^a	−0.506656 (n/a)	0.983046 (n/a)	6
Southern (3319)	0.843941 (0.158047)	−0.823358 (0.10155)	0.992617 (0.0022)	13

The northern sample taken from Bragg (2001) represents 5 yr (rather than annual) increment (divide the results by 5 to arrive at annual value). Final *n* as described in Table 2.

^a It was not possible to annualize the standard error estimates.

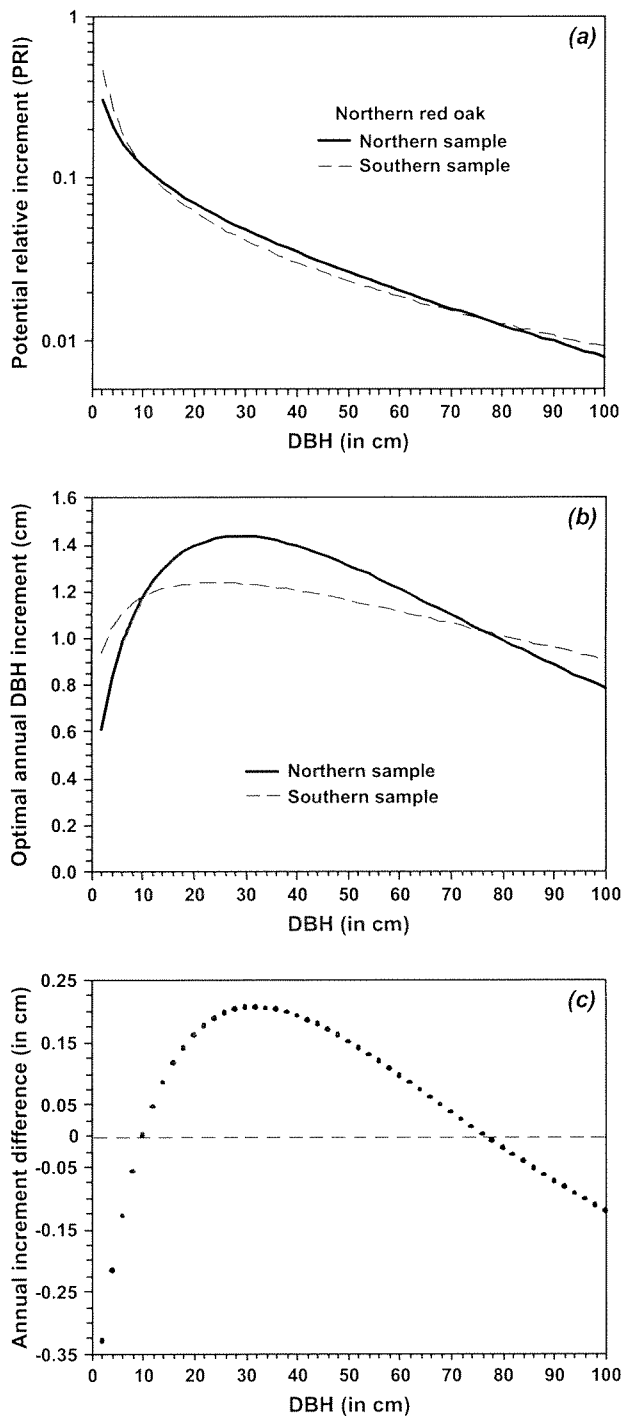


Fig. 10. PRI curves (a), optimal annual DBH increment (b), and difference between increments (c) for northern red oak comparing Lake States (Michigan, Minnesota, and Wisconsin) and Midsouth (Arkansas, Louisiana, Missouri, and Oklahoma) regional models.

3.3.3. Intraspecific differences across broad geographic regions

Northern red oak PRI curves from distinct geographic regions produced notably different model behavior (Table 4, Fig. 10a). Midsouth-origin (Arkan-

sas, Louisiana, Missouri, and Oklahoma) northern red oak had the potential to grow faster at small (2–10 cm DBH) and large (>75 cm DBH) sizes, while optimal growth potential was predicted to be higher from 10 to 75 cm DBH in the Lake States (Michigan, Minnesota, and Wisconsin) model. Over the diameters considered, the Midsouth model displayed less range in increment than the Lake States model (Fig. 10b). Rarely were these differences very pronounced, however, varying from ± 0.2 cm annually. Given that predicted northern red oak increment varied from 0.6 to 1.4 cm (Fig. 10b), this would translate into a 14–33% difference, depending on the model used (Fig. 10c).

4. Conclusions

This paper describes potential challenges in the development and interpretation of PRI increment models. For example, depending on which state inventory was used, different model parameters were produced for both loblolly and shortleaf pine, which in turn changed optimal growth patterns. Whether or not this signified regional variation, lack of suitable examples, uncertainty in model fitting (point selection), or some other factor cannot be distinguished with the available information. Pooling inventory data from adjacent states can assist in PRI derivation by reducing uncertainty and expanding the sampling conditions and DBH range. The benefits gained by supplementing sample sizes, especially for uncommon species, probably outweighs the loss of site-specificity.

Differences in the shape of the curves between northern and southern samples of northern red oak suggest that regional differences in performance exist and should be considered when developing PRI models. It is not clear if this would preclude extensive pooling of inventory information, but it would certainly argue against using regression models developed for one part of the country (e.g., the Lake States) in a very different region (e.g., the Midsouth). Care should also be taken in fitting PRI models if genetically improved plantations are included in the sample, especially when compared to natural forests. Models developed without segregating stands by their source may yield biased predictions of optimal increment (especially at smaller diameters). While no major differences by stand origin for Arkansas loblolly arose, intensively cultured species may benefit from having two models developed: one for improved plantations, the other for stands of natural origin.

Generally, the challenges facing the PRI approach are the same as experienced in other optimal model designs: the acquisition of reliable and extensive data, avoidance of bias in model fitting, and the development of a system that best reflects empirical, ecological, and

physiological considerations. Notwithstanding the uncertainty associated with EFIDB data and the origin and management of stands, the PRI methodology links empirical information with the key concepts related to optimal diameter growth prediction. Furthermore, it may also be possible to improve some aspects of PRI derivation by using curve fitting techniques that are less sensitive to traditional ordinary least squares regression assumptions.

Acknowledgements

I thank the following for their helpful commentary on this manuscript: Kurt Gottschalk (USDA Forest Service, Northeastern Research Station), Jim Guldin (USDA Forest Service, Southern Research Station), Dave Larsen (University of Missouri at Columbia), Tom Lynch (Oklahoma State University), and Boris Zeide (University of Arkansas at Monticello). Several anonymous reviewers helped improve the quality of this manuscript.

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